

Sex, Mate Selection, and Evolution

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Abstract: Simulations of the evolution of populations of diploid organisms showed that mate selection strategies which selected for “good genes” and strategies based on assortative mating, confer a much higher average fitness and higher evolutionary stability to populations than random mating. This advantage was more conspicuous the more genes per organism were simulated and the more genes were involved in the phenotype screened for mate selection. The results suggest that the evolutionary advantage of mate selection becomes evident only when the simultaneous adaptation of several genes are simulated. A cautionary lesson from the model is that mating is not likely to be random in nature and that mate selection may direct evolution by accelerating the exposure to natural selection of relevant traits. That is, models assuming random mating may not reflect what is happening in nature as sexual reproduction is probably associated with mate or gamete selection in most living organisms.

Introduction

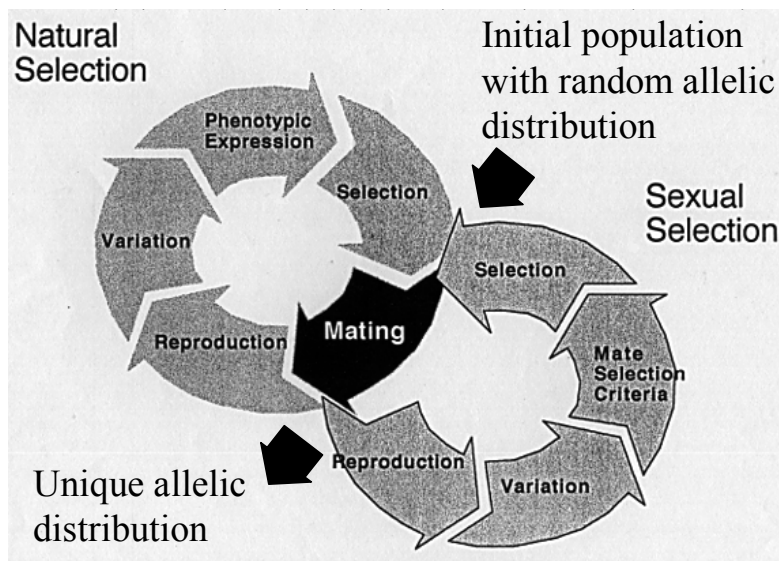
“What selective forces maintain sexual reproduction and genetic recombination in nature?” (27). Unfortunately, this remains an open question in evolutionary biology (23). Asexual reproduction has three theoretical advantages: (i) parthenogenetic females do not need to find mates, (ii) they produce twice as many daughters and four times as many granddaughters compared to the average sexual ones, and (iii) natural selection drives adaptation and thus selection of relevant traits much faster in asexual organisms compared to sexual ones (20). Despite these relative theoretical advantages of asexuality, most higher organisms are sexual. The main hypotheses put forward to explain this mystery (17) can be grouped into three categories:

- 1- The ecological genetic models which postulate that sex is adaptive in variable environments because it enables the rapid spread and creation of advantageous traits (4,10,14,16), which includes the “Red Queen” hypothesis as a mechanism to escape parasites, based on the pioneering works of Bremermann (5,6) and Hamilton (13).
- 2- The mutation-accumulation models, which suggest that sex (15,29,30) and/or ploidy cycles (20,24) are adaptive because they perform the efficient removal of deleterious genes.
- 3- The mate selection model (8,20) which assumes that mate selection made possible by sex, allows the selection of “good genes” before these genes develop phenotypes which will be selected by natural selection, orienting the evolutionary process towards the fixation of these beneficial traits. A variant hypothesis (3)

assumes that the cheaper sex to produce (generally the males) suffers stronger selection pressures. Only individuals with good survival abilities reproduce, so that the mate selection criteria would relate to an increased survivorship.

These hypotheses may complement each other, but here I explore hypothesis No. 3 in more detail.

Figure 1: Schematic representation of the model showing how, through the interaction between natural and sexual selection, populations of virtual individuals tend to obtain unique allelic distributions characterizing the various genes defining the organisms.



Although there is little evidence for mate or gamete selection in species reproducing sexually, there is no evidence for the absence of it in any sexual species. Thus, sexual reproduction without previous mate or gamete selection may be rare. Indeed, even yeast have been suggested to have mate selection (31). Courtship is normally thought to assure that mates are of the same species and of different sex. However, most organisms have courtship behavior which seems too elaborate to serve only this purpose (1,9). Thus, Darwin offered the concept of sexual selection, which has acquired a variety of meanings (2). The effect of mate selection systems on biological

evolution may be very complex and is not easily characterized using analytical models (28). Most analytical models found in the literature fail to capture relevant properties of complex biological systems (26). On the other hand, analytical models are limited in the degree of complexity they are able to tackle due to limitations in the available mathematical tools. To avoid these limitations, evolutionary computer simulations (sometimes referred to as “artificial life”) have been developed for studying evolutionary dynamics (28,33). Regarding sex, studies based on simulation models (8,20), showed that sexual reproduction in virtual populations with differentiated male and female organisms, could be maintained through evolution only if mate selection was present. Mate selection was proposed as a fundamental step of the evolutionary dynamics (Fig. 1), which accelerates evolution by focusing natural selection to the appropriate phenotypes and genes. Thus, simulation models seem to be, for the moment, the best tool available for the theoretical study of the interaction between mate selection and natural selection, allowing the study of features which are not evidenced when studying these systems on their own, but which may emerge as a result of their interaction.

Methods

To assess the possible impact of mate selection on evolution, I explored the effect of a variety of mate selection criteria on the evolutionary dynamics, using a simulation model which had better precision than analytical models in explaining experimental data regarding the emergence of genetic resistance to antibiotics and pesticides (22). The model attempted to limit simplifications by studying the effect of various simultaneous selection pressures on populations of organisms with up to 16 different genes. A more detailed description is found elsewhere (19,20). Two types of virtual organisms were simulated: “Simple” organisms with allelic variance in 7 genes (see Table 1) and “complex” ones with allelic variance in 16 genes. The evolutionary algorithms affecting the genes listed in Table 1 were:

Mate selection: Females choose males depending on their allelic value of the mate selection criteria (MSC) gene, as indicated in Table 2. Females not finding the appropriate male mated with the one closest to the criteria searched for. If no male of the species was encountered, the female did not reproduce during that time step. The mate selection strategies simulated can be grouped into four categories: (i) no selection of mates or random mating (coded by allele 0 of gene 8 as indicated in Table 2), (ii) females prefer males whose phenotype signals “good genes” (coded by alleles 1 to 3), (iii) assortative mating in which females prefer males with the genetic constitution most similar to hers (coded by allele 4 in Table 2), and (iv) dissortative mating in which females prefer to mate with the genetically most dissimilar male (coded by allele 5).

Reproduction: Mated individuals transmitted their genes to the offspring according to the rules of bisexual diploid reproduction (i.e. meiosis), with a probability for crossover of 0.5, so that they received a mix of genes from both parents.

Table 1: Genes defining the organisms simulated. Genetically complex organisms had allelic variance in all 16 genes, simple ones in only the first 7 or 8, and default values (in parenthesis) for the rest.

Gene	Alleles	Effect on phenotype
1	0-10	Maximum life spans ranging from 0 to 10 time steps
2	0-10	Maximal clutch size
3	0-5	Minimum reproductive age for females
4	2	Sex, either male or female
5	0-10	Sex appeal of males in an increasing range of attractiveness
6	0-10	Resistance to biocide 1. Only allele 0 was resistant to that particular biocide
7	0-10	Resistance to biocide 2. As for gene 6
8	0-11	MSC or criteria for mate selection (Table 2)
9	0-5	Minimum reproductive age for males (1 t-step)
10	0-10	Mutation probability coding for mutation rates from 0.2 to 10^{-7} mutations in logarithmic increments (0.001)
11	0-10	Mutation intensity for new mutated values, ranging randomly from 0 to the maximum allelic value (10)
12	0-1	Sex determination mechanism, either random (0) or weighted according to value of gene 13
13	0-10	Sex ratio of newborns (5 = 1 male/female)
14	1-100	Number of males screened by females in search of potential mates (100)
15/16	0-10	Neutral gene whose phenotypic expression did not affect the fitness of the organism (0).

Variation: Randomly selected genes mutated their allelic value with either a fixed probability over the total allelic range (default values for genes 10-11 in Table 1) or with a genetically determined probability (probabilistic frequency of mutations) within a given allelic range (mutation intensity), depending on the allelic value of genes 10 and 11 in Table 1. The existence of genes determining mutation rates have been proposed (25) and can be simulated here.

Phenotypic expression: Allelic dominance was simulated as is often done in genetic algorithms (11). That is, only one of the two alleles in each individual, chosen at random, was expressed phenotypically.

Two life history traits were simulated, trying to copy what is known for most real organisms:

- 1- The final clutch size of individuals was calculated based on the allelic characteristic of the gene coding for clutch size and the age of the reproducing individual, using a normal distribution, so that the maximal clutch sizes were partially predetermined genetically and occurred at an optimal age of reproduction.

- 2- Clutch sizes affected the probabilities of survival of the offspring, so that individuals born in clutches larger than optimal decreased their probability of survival exponentially.

Table 2: Algorithms evoked by the allelic values of the gene for mate selection criteria (MSC: gene 8 in Table 1) in females selecting conspecific males

MSC	Mate selection strategy coded
0	Random mating
1	Females prefer males with low values of gene 6 in Table 1 which are more likely to be resistant to biocide 1. Selection of one “good gene”
2	Females prefer resistant males for both biocides, selecting for low values of genes 6 and 7. Selection of two “good genes”
3	Females prefer males with appropriate allelic values in genes for maximum life span, clutch size, reproductive age and the two resistance genes. Selection of 5 “good genes”
4	Females screen the allelic values of males and chose those with an allelic composition most similar to hers. Assortative mating
5	Similar to MSC 4, but females prefer males with the most dissimilar alleles. Dissortative mating.

Selection: In order to simulate the action of various selection forces acting simultaneously, individuals were excluded from the population:

- 1- When their age exceeded their genetically determined life span.
- 2- When randomly selected by density independent and density dependent criteria with a probability that increased with population density.
- 3- When parents clutch size exceeded optimal sizes at high population densities.
- 4- When biocides (i.e. illness or any agents killing selectively) randomly trimmed the population from individuals not possessing the resistant phenotype.

The intensity of selection forces 1, 3 and 4 could be affected by the expression of mate selection criteria 1-3 in Table 2.

Two different types of experiments were performed.

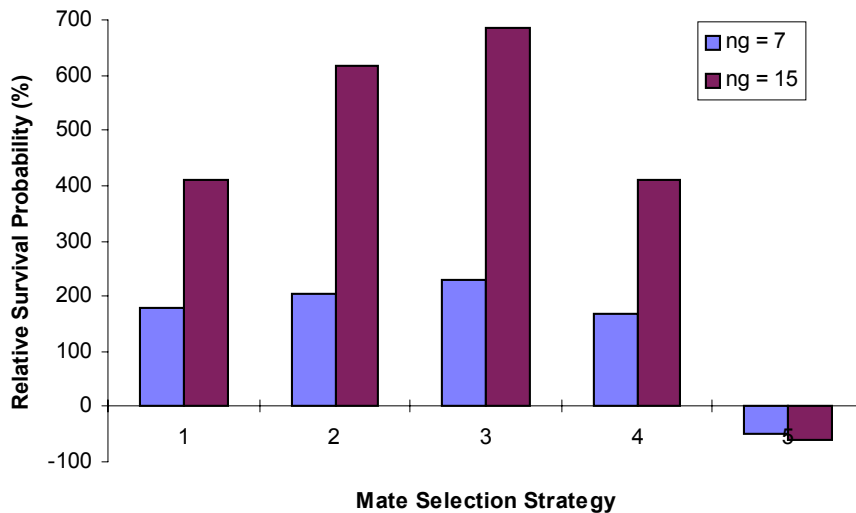
- 1- Survival probabilities of “isolated populations” were assessed by randomly creating initial populations in which all individuals had the same mate selection strategy and evaluating the probabilities of these populations to survive variable environments for a given number of time steps.

2- Simulation of “gene selection” aimed at assessing the effect of selection on the allelic distribution of a given gene in a single interbreeding population. Here, different mate selection strategies were assigned initially at random and the frequency in the population of the various alleles coding for a specific mate selection strategy were monitored.

Results and Discussion

Of the mate selection criteria tested, those showing the most interesting results are given in Table 2. The effect of each of these mate selection criteria on the evolution of diploid organisms is shown in Figures 2 and 3.

Figure 2: Probability of survival of the “isolated populations” in which all individuals used a single mate selection criterion. The results of these two series of simulations are expressed as the percentage difference in relation to the probability of survival of populations using random mating. Mate selection criteria used are indicated in the ordinate and correspond to the MSC given in Table 2. Each series, comprising 250 simulations run for 30 time steps for each MSC, represent organisms with different genetic complexity as indicated by the number ng genes (ng) in Table 1 which had allelic variance. Gene 8 was fixed for each simulation at the value indicated in the ordinate.

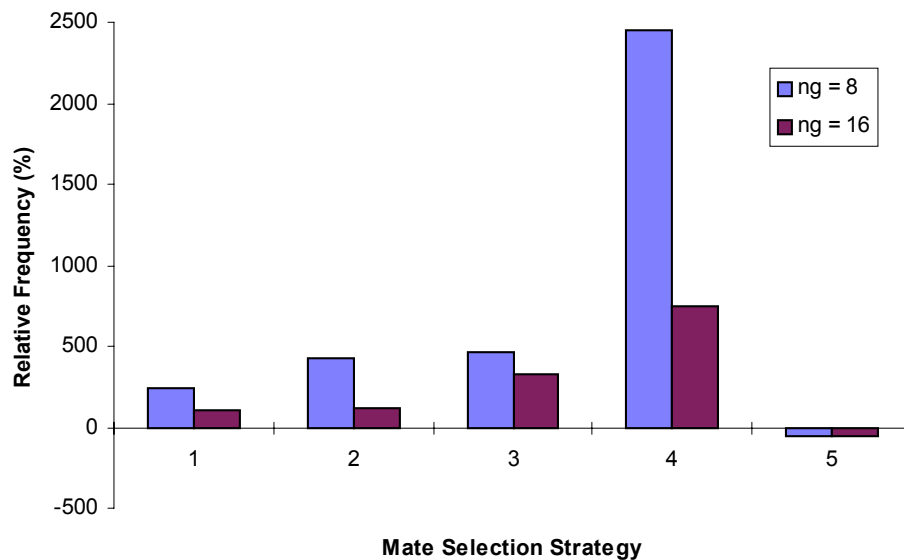


Strategies in which females choose males according to their beneficial genetic traits (MSC 1-3), and those in which females screened males for similar genes (MSC 4) outperformed random mate selection in both types of evolutionary experiments.

Choosing genetically different males under-performed random mating. Assortative mating (MSC 4) dominated in simulations of gene selection (Fig 3), but not in simulations of isolated populations (Fig 2). This phenomenon will be analyzed in more detail elsewhere, but I suggest that assortative mating is successful with gene selection because it reduces excess genetic variability (slower so among complex organisms), it avoids fit females diluting their advantageous genes during reproduction, and it accelerates the extinction of suboptimal alleles, reversing the Muller's ratchet (29,30,15). The strong effect on evolutionary stability of assortative mating confirms previous findings suggesting the power of assortative mating in allowing the maintenance of sex (8).

Increased genetic complexity of organisms increased the benefits of mate selection relative to random mating (Fig 2). The model simulated up to 16 genes, yet real organisms have many more. It is difficult to assess the impact mate selection may have on the evolution of highly complex organisms, but the results suggest that analyses modeling few genes may not show the effect on the evolutionary dynamics that mate selection have. Traditionally, models of biological evolution are based on simulations of haploid organisms with one or two genes (4,11,14,16 for example), which is clearly insufficient to reflect the biological relevance of mate selection. Mating is not likely to be random in nature, although random mating is commonly assumed in theoretical studies in biology (4 for example). The results here showed that several mate selection strategies confer higher fitness and have a higher evolutionary stability than random mating. Selection criteria which increase the odds of mating with a fitter mate are very successful and should be a common feature in real organisms. This seems to be the case, as an ever larger number of examples of mate and sperm selection based on secondary sexual characters as fitness indicators, accumulate (1,9), in addition to evidence that secondary sexual phenotypes are indicative of the harmonic working of a large number of genes (18 for example). Strategies based on assortative mating, in which genetically similar mates reproduce, should also be common in nature (8). Few cases have been thoroughly explored, but evidence for assortative mating among humans seem to be strong (7,12,21,34-37).

Figure 3: Average allelic frequency of populations when “gene selection” was simulated. Individuals coded and evolved their mate selection strategy according to the allelic value of the gene for MSC in Table 2. Frequencies of the alleles are expressed as the percentage difference in relation to the frequency of the allele coding for random mating. Else as in Figure 2.



The model confirmed previous findings showing that mate selection increases the evolutionary viability of sexual species significantly (8, 20). These previous findings suggested that sexual reproduction with random mating is evolutionary unstable vis a vis asexual reproduction. The present results showed that the stronger the mate selection for “good genes” the more successful the sexual species. This suggests that secondary sexual characters used for mate selection should be affected by many different genes. This seems to be the case of symmetry as a character used for mate selection in humans (32). A falsifiable prediction is that sex pheromones for example, should have a role in mate selection and be influenced by a large number of genes. That is, a large number of enzymes should be involved in the accumulation, release and/or biosynthesis of compounds or blends of compounds constituting sex pheromones, most of which should also have a role in other unrelated physiological processes.

Acknowledgments: I thank G. Ochoa, C. Bosque, J.V. Hernandez, E. Herrera and three anonymous referees for critical comments.

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